

# An Ethogram of Body Patterning Behavior in the Squid *Loligo vulgaris reynaudii* on Spawning Grounds in South Africa

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**Abstract.** Squids are capable of a high degree of visual signaling, most of which is expressed through the neurally controlled chromatophore organs in the skin. An accurate catalog (or ethogram) of these signals is an essential prerequisite to quantified behavioral analyses and experimentation. Body patterns such as those described here may also be useful for distinguishing between morphologically identical species or subspecies of commercial importance. The natural behavior of *Loligo vulgaris reynaudii* on spawning grounds was filmed by divers, and the body patterning repertoire was described in detail; 23 chromatic components, 4 postural components, and 9 locomotor components of body patterning were observed and correlated with different types of behaviors. Most of the chromatic components were expressed during intraspecific behaviors (e.g., agonistic behavior among males, courtship, mating) and, to a lesser extent, during interspecific interactions with fishes. Several of the most basic types of body patterns are described, the most distinctive of which are Lateral Display and White Flashing used between males in agonistic contests. This species is comparable to other *Loligo* spp. in its complexity of body patterning behavior.

## Introduction

Cephalopods have evolved a chromatophore system unique in the animal kingdom: because the pigmented cells in the skin are under neuromuscular control, skin color and pattern can change rapidly, resulting in a high diversity of appearances in individual animals. Much of the behavior of cephalopods is expressed through these

pattern and color changes of the body, which convey visual signals to conspecifics, predators, and prey (e.g., Moynihan and Rodaniche, 1982; Hanlon and Messenger, in press). These “body patterns” are made up of *chromatic* (i.e., color), *textural*, *postural*, and *locomotor* components (cf., Packard and Sanders, 1971; Packard and Hochberg, 1977; Hanlon, 1982; Hanlon and Messenger, 1988). Chromatic components are discrete neural entities, just as postural, locomotor, and textural components are. That is, the expression of Dark head and arms, for example, represents the selective neural excitation of motor neurons in the CNS that control the expansion of all chromatophores on the head and arms. A wide variety of body patterns can be exhibited by each individual of each species; patterns are not only species-specific, some are also sex-specific.

Our aim in this paper is to describe an ethogram for the commercially important squid *Loligo vulgaris reynaudii*. An ethogram is a catalog and description of behaviors and is used as the basis for studying behavior. In cephalopods, the development of a system of names for the components of body patterning, combined with careful illustration and description of each one, is mandatory for at least three types of studies: (a) accurate and quantitative analyses of behavior (e.g., Moynihan and Rodaniche, 1982; DiMarco and Hanlon, in prep.; Hanlon and Messenger, unpub.), (b) developing taxonomic keys to species identification (Hanlon, 1988; Roper and Hochberg, 1988), and (c) comparing conserved characters of chromatic expression that can aid phylogenetic studies (e.g., Moynihan, 1985; Hanlon, 1988; Burghardt and Gittleman, 1990).

*Loligo vulgaris reynaudii* (D’Orbigny) attains average adult sizes of 23 cm mantle length for females and 32 cm

for males, and is an important commercial species in South Africa, with up to 10,000 tons caught annually by hand jigging (Augustyn, 1990, 1991; Sauer *et al.*, 1992). This paper is part of a broader study of the biology and life history of the species; the long-term goal is to acquire adequate information to manage the fishery properly (Augustyn *et al.*, 1992, 1994). Previous studies included preliminary behavioral observations from video footage taken by a small, remotely operated vehicle (ROV). One of these studies (Sauer *et al.*, 1992) revealed glimpses of rather complex signaling related to spawning behavior, which led to the present investigation.

### Materials and Methods

Behavior can be observed directly and at close range because squids habituate to divers within a few minutes; a close approach is facilitated if the divers move slowly or are immobile. During 33 dives throughout daylight hours, nearly 11 hours of squid behavior were observed from 11 November to 1 December 1993 on spawning grounds in depths of 17–30 m. The study area was between Port Alfred in the east (33°36'87 S, 26°55'51 E) and the Tsitsikamma Coastal National Park in the west (34°01'81 S, 23°56'43 E), or about 700 km east of Cape Town. Over 4 of the 11 hours of behavior were recorded with a Sony TR81 Hi-band 8-mm video camera in an underwater housing. An additional 1.3 hours of videotape from previous years were also reviewed (filmed by W. Sauer and G. Fridgeon from 1989 to 1992 in the same areas). Drawings from the video images were made with the software program CoreDRAW for DOS.

Video sampling (Martin and Bateson, 1993) was accomplished as follows. During the early dives, sampling was *ad libitum* with continuous recording because we sought preliminary data that would reveal the variety of behaviors observable with hand-held cameras; approximately half our recordings were *ad libitum*. After analyzing these tapes on board ship, we switched to behavior sampling, in which a group was watched and only particular behaviors were recorded (*e.g.*, agonistic bouts, mating, fish interactions, *etc.*); about a third of the recordings were such behavior samples. The remaining recordings involved focal sampling, in which we followed and taped an individual squid (*e.g.*, a lone male, a paired female, a sneaker male, *etc.*) or a dyad (*e.g.*, a courting pair and any competing males). Analyses involved many replays of the recordings by all coauthors, so that each type of information sought could be obtained (*e.g.*, one replay for observing components, one for describing them, one for counting them, one for describing mating, *etc.*). The time spent on total analysis thus totaled several hundred person-hours.

### Terminology

A **Body Pattern** is the overall appearance of the cephalopod at any moment, and it is made up of one or more of the following **Components**: chromatic (*i.e.*, color), textural, postural, and locomotor. Textural components refer to skin papillation in cuttlefishes and octopuses, but squids do not have this ability. For convention, components are capitalized in the first word only, while body patterns are capitalized at the beginning of each word. Names of components and of body patterns follow existing cephalopod literature (reviewed by Hanlon and Messenger, in press). Emphasis was given to naming components and body patterns as morphological descriptors to avoid behavioral or functional connotations. Following the tradition in ichthyology and herpetology (Robins *et al.*, 1991), the terms "stripe," "line," or "streak" mean longitudinal chromatic components that parallel the body axis, whereas "bar" or "band" mean transverse or vertical components.

### Results and Discussion

Table 1 lists the components and body patterns of *Loligo vulgaris reynaudii*. The chromatic components are illustrated in Figure 1. Unless stated otherwise, all components and body patterns were shown by both sexes.

The body patterns and components listed in this ethogram constitute a subset of all squid behaviors, and they reflect only the types of behaviors we sampled for and the behaviors that happened to occur on those dives on those days in the immediate vicinity of the egg beds. Although numerical quantification is not appropriate for this study, we list in parentheses, in Table 1, the number of times (*n*) that we counted a body pattern or component on video tapes to give the reader an impression of how common some of them are.

#### Light chromatic components

Only three were observed, and each is common to all *Loligo* spp. **Clear** is characterized by retraction of all chromatophores, rendering the animal whitish or translucent. This component can act alone as a body pattern, and it is the most common pattern in calm, undisturbed squids. Two iridescent components, both thought to aid in crypsis, were also observed: **Dorsal mantle collar iridophores** and **Dorsal mantle splotches**; these are not illustrated but can be seen in color plates in Hanlon (1982).

Males show the **Accentuated testis** component. Accentuation of this white organ is accomplished by expansion of most mantle chromatophores while simultaneously there is selective retraction (*i.e.*, lack of neural excitation) of the chromatophores over and even be-

yond the border of the testis. Males of other loliginid squids also have this capability (Hanlon, 1982, 1988; Moynihan, 1985), which is thought to be an expression of "maleness," although this has not been demonstrated. *Loligo vulgaris reynaudii* shows the component to other males and to females.

The white **Accentuated oviducal gland** of females is similar in appearance to the Accentuated testis of males, but is different in shape, position, and frequency of expression. On rare occasions, females show a white area directly over the eggs in the most posterior dorsal mantle.

#### *Dark chromatic components*

*Loligo vulgaris reynaudii* has three color classes of chromatophores: yellow, red, and brown. All **dark** is characterized by expansion of all chromatophores, resulting in a reddish-brown overall color. This component, which also acts independently as a body pattern, is an expression of alarm or disturbance in the squid. For example, close unexpected approaches of fishes (even small nonpredatory ones) cause brief expression of All dark, but the pattern is also used intraspecifically during agonistic encounters, and even between males and females, when one or the other is startled (Hanlon, 1982; Hanlon *et al.*, 1983; this study). There is a distinctive unilateral variation in which one side of the entire arms, head, and mantle (but usually not the fins) becomes dark, illustrating a striking bilateral asymmetry. Another variation of All dark is **Dark fins**, giving the impression that the posterior half of the mantle is darkened. Conversely, **Dark head and arms** shows the opposite effect, and there is a variation of this in which only the arms are darkened; these components are seen during intraspecific agonistic encounters. Dark head and arms is also exhibited by *Loligo opalescens*, but in that species it is seen during mating (Hurley, 1977). Occasionally, males show **Dark tentacle or arm tips** but the significance of this component is unknown; on occasion when Raised arm (see below) is used during agonistic contests, males darken the arm tip. **Shaded eye** aids in crypsis by covering the bright iridescent sclera of the eyeballs and is common among loliginid squids.

The only transversely oriented component is **Bands** (called Rings in previous literature), which are common in loliginids and are associated either with (a) crypsis through disruptive coloration (as in *Loligo pealei*; Stevenson, 1934) or with (b) secondary defense, in which a squid approached closely by a predator (or possibly a large object like an ROV with shining lights) shows disruptive coloration, often with some distinctive arm posture (Sauer and Smale, 1993). This component functions alone as a body pattern, but has rarely been seen thus far, and no comments are yet appropriate.

*Dark striped components.* *Loligo vulgaris reynaudii* shows five striped chromatic components. **Dark dorsal stripe** is common to *Loligo* spp. and is seen in calm squids; the stripe varies in width from a few millimeters to one-third of the mantle width. It is thought to aid in crypsis through countershading when viewed laterally and through disruptive coloration when viewed from above, by covering some of the bright organs such as the testis, oviducal glands, and ink sac (Hanlon, 1982, 1988; Hanlon and Messenger, in press).

The next four striped components are used during intraspecific agonistic encounters. **Fin stripe** occurs when squids appear to be mildly alarmed during agonistic contests; also, the component is observed commonly on squids that have been jigged and brought into the boat (a highly unnatural situation to which no function can be ascribed, although this is presumably an extreme form of stress and alarm). **Mantle margin stripe** is very common among *Loligo* spp. and is usually shown posteriorly as a dark red line below the fin insertion. However, it is occasionally shown as a longitudinal dark red line from the fin insertion forward to the mantle collar. It is also a mild reaction to disturbance or alarm from intraspecific encounters. **Arm stripe** is seen in similar situations, but is quite uncommon: either the first or third pair of arms is darkened. **Ventral mantle stripe** is analogous to the "Mid-ventral ridge" of *Loligo plei* (Hanlon, 1982) except that there is not the extrusion of skin that produces the ridge in *Loligo plei*. The function is unknown in *L. vulgaris reynaudii* or in *Loligo forbesi* (Porteiro *et al.*, 1990), except that in the present observations males showed this component often while swimming alongside a mate. It can be seen only from below, but this may be important because males often swim slightly above their female mate. The possibility that the stripe helps disrupt the body shape when viewed from below (by predators) should not be discounted.

*Dark spotted components.* These three components are expressed during alarm or threat situations, mainly intraspecifically, and are often shown unilaterally on the side towards the other squid. **Arm spots** are small and can occur either on the base of the second or third arms, whereas the **Infraocular spot** occurs roughly between the eye and the Arm spots. Both are sometimes expressed simultaneously. There is considerable variation in the expression of the "spot," as illustrated. **Fin spots** are about 5 mm in diameter in large adults and are distributed as illustrated; they are expressed commonly during agonistic contests between males.

*Dark components associated with reproduction.* In addition to Accentuated testis and Accentuated oviducal gland, four other components are related to sexual behavior.

Table 1

Body patterns and their components in the squid *Loligo vulgaris reynaudii* (f = female, m = male); (n) is the number of times each component was observed on video. Compare Figure 1

Chromatic components			
Dark:	n =	Light:	n =
1. All dark	(87)	1. Clear	(356)
2. Dark dorsal stripe	(76)	2. Dorsal mantle collar iridophores	(50)
3. Ventral mantle stripe	(25)	3. Dorsal mantle splotches	(>50)
4. Mantle margin stripe	(136)	4. Accentuated oviducal gland (f only)	(149)
5. Fin stripe	(34)	5. Accentuated testis (m only)	(46)
6. Arm stripe	(83)		
7. Fin spots	(52)		
8. Arm spots	(75)		
9. Infraocular spot	(57)		
10. Dark fins	(56)		
11. Bands	(2)		
12. Shaded eye	(41)		
13. Dark head and arms	(98)		
14. Dark tentacle or arm tips	(30)		
15. Lateral mantle streaks (m predominantly)	(84)		
16. Red accessory nidamental gland (f only)	(2)		
17. Shaded oviducal gland (f only)	(9)		
18. Lateral blush (f only)	(34)		
Postural components:		Locomotor components:	
1. Raised arm	(48)	1. Inking	(6)
2. Downward V curl	(2)	2. Jetting	(>100)
3. Splayed arms	(42)	3. Parallel positioning	(>25)
4. Egg holding (f only)	(22)	4. Fin beating (m only)	(>10)
		5. Jockeying and Parrying	(23)
		6. Head-to-head mating	(0)
		7. Male parallel mating (m only)	(10)
		8. Male "sneak" mating (m only)	(10)
		9. Mate guarding (m only)	(>100)
Body Patterns			
Chronic patterns: (minutes-hours)		Acute patterns: (seconds)	
1. Clear	(356)	1. White Flashing (m)	(>182)
2. Dorsal Stripe	(76)	2. Dark Flashing	(32)
		3. Accentuated Oviducal Gland (f)	(149)
		4. Accentuated Testis (m)	(46)
		5. Bands	(2)
		6. Blanch-Ink-Jet Maneuver	(3)
		7. Lateral Display (m)	(>30)

Three are shown only by females. Females can mask Accentuated oviducal gland with the component **Shaded oviducal gland**; this is particularly effective when the squid is in the otherwise Clear body pattern because, as noted often by divers and from video recordings, it decreased conspicuousness of the very white oviducal gland. The **Red accessory nidamental gland** is large and bright in this species and can be seen through the mantle, either from below or laterally. Thus it must be considered a potential signal in communication, even though it is internal. Its primary anatomical function is unknown, but it may be a sign of female sexual maturity since it turns red only

upon attainment of full maturation (Drew, 1911; Hanlon, 1982). Finally, females show a **Lateral blush** component that may be analogous to similar components in other loliginids, for example, the Lateral blush of *Loligo plei* (see Hanlon, 1982), the Pied pattern of females of the Caribbean reef squid *Sepioteuthis sepioidea* (see Moynihan and Rodaniche, 1982) and the Lateral mantle spot in female *Lolliguncula brevis* (see Dubas *et al.*, 1986).

**Lateral mantle streaks** are basically male-only streaks of chromatophores, each streak from 2–24 mm long and surrounded by a clear area of about 1–2 mm that is completely devoid of chromatophores, thus rendering the

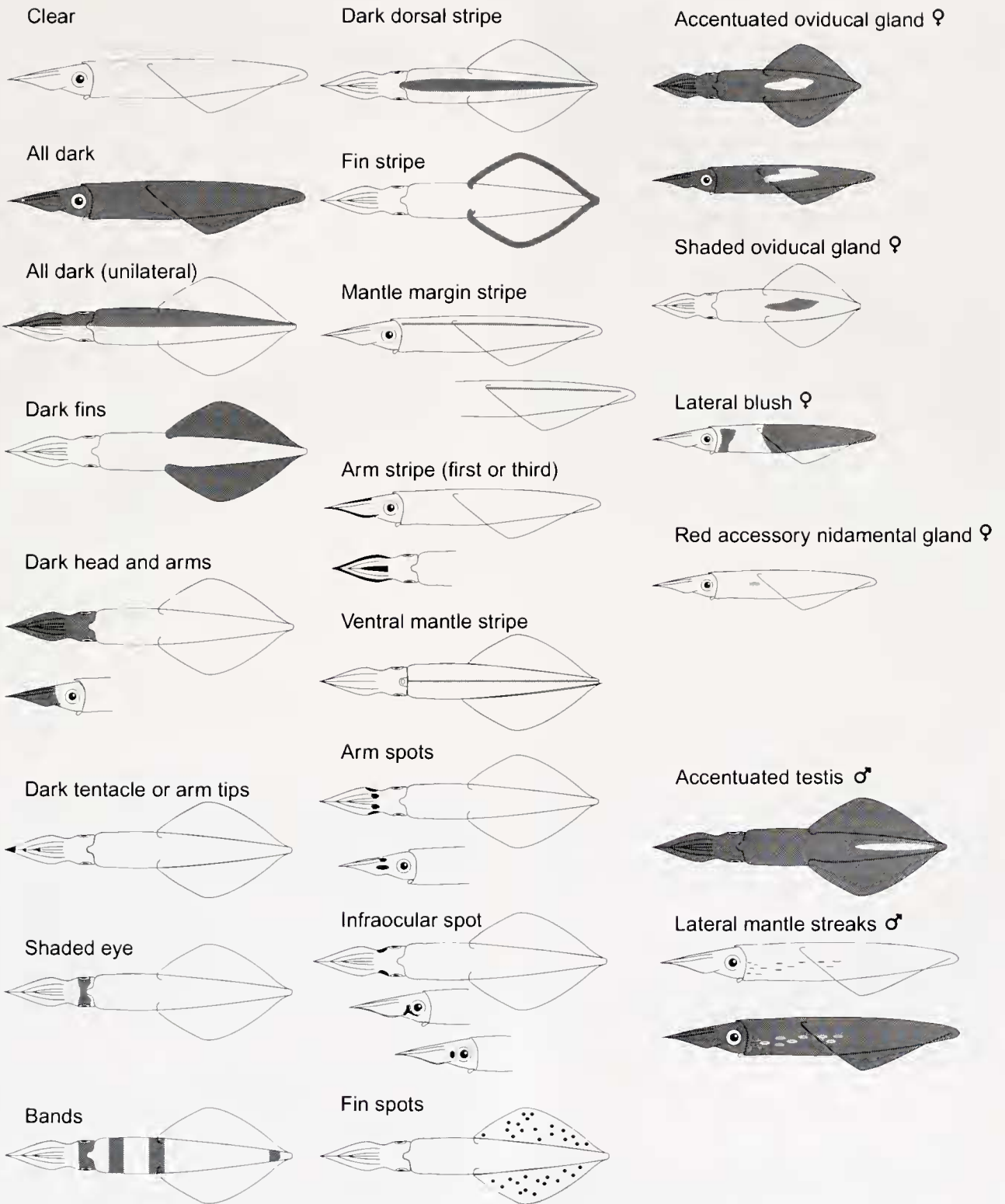


Figure 1. Neural expression of the chromatic components of body patterning in the squid *Loligo vulgaris reynaudii*.

streaks more obvious relative to surrounding chromatophores. A sample of the number and distribution of these streaks is given in Table II. Large mature males have 8–17 streaks, whereas mature females have only 1–3 streaks, but in females they occur only in the largest animals and are very small and almost certainly insignificant for visual signaling, being so small and indistinct. In all cases, most of the streaks are located anteriorly (see Fig. 1). In a typically sized streak of ~16 mm long in a male, there are about 320 chromatophores, whereas in a typical streak of 4 mm length in a female there are only 29 chromatophores. The morphological arrangement of chromatophores in the streaks differs from that on the rest of the animal. The arrangement is similar to the "Yellow-Brown Discoid Unit" in *Loligo plei* (Hanlon, 1982); that is, there are only two color classes of chromatophores instead of the customary three. The streaks are similar in appearance to the Lateral flame component in *Loligo plei* and *Loligo pealei* (Hanlon, 1982; Hanlon et al., 1983) and to the Lateral mantle streaks in *Loligo vulgaris vulgaris* and *Loligo forbesi* (Hanlon, 1988). However, there seems to be a major difference in the way they are used behaviorally, because in *Loligo vulgaris reynaudii* they are not used during the Lateral Display (see below), whereas in *Loligo plei* they are a major component during Lateral Displays (Hanlon, 1982; DiMarco and Hanlon, unpub.).

Taxonomically it may be important that the streaks in male *Loligo vulgaris reynaudii* are shorter than those in male *Loligo forbesi*, even on a proportional scale. For example, *Loligo vulgaris reynaudii* in the range of 14–38 cm mantle length had streaks 4–13 mm long, whereas *Loligo forbesi* in the same size range had streaks 10–30 mm long (from Table 3 in Hanlon, 1988). Furthermore, female *Loligo vulgaris reynaudii* have only one or a few inconspicuous streaks, whereas female *Loligo forbesi* have 8–12 streaks on each side of the mantle, each about 14 mm long; these latter streaks were easily visible in the skin unlike those of *Loligo vulgaris reynaudii*. This may be a distinguishing character in both sexes and should be checked carefully in *Loligo vulgaris vulgaris* as a possible diagnostic character with which to separate *Loligo vulgaris vulgaris* from *Loligo forbesi* in their widely overlapping ranges off European coastlines.

#### Postural and locomotor components

**Inking** is the expulsion of ink mixed with mucus. It takes two basic forms: (a) relatively small puffs either in the form of a pseudomorph that resembles the size and shape of an escaping squid, or more commonly just a general blackened spot; or (b) large and dense clouds of ink. **Jetting** refers to rapid body movement by expulsion of water from the funnel (*i.e.*, jet propulsion), usually only about 1 m in distance and usually backwards. There is

Table II

Number and length of the chromatic component Lateral mantle streaks on the mantle of the squid *Loligo vulgaris reynaudii*. Measurements in mm

	Mantle length	No. streaks per side		Mean streak length and (range)		
		Left	Right	Left	Right	
Males:	1	138	11	9	3.9 (2–6)	4 (3–5)
	2	142	9	9	3.6 (2–5)	4 (2–6)
	3	170	11	9	4.8 (4–7)	4.2 (3–6)
	4	196	8	9	6.5 (3–9)	5.9 (4–8)
	5	212	8	8	6 (5–7)	5.4 (4–8)
	6	215	14	8	5.8 (3–11)	7 (5–10)
	7	220	6	5	5.8 (4–8)	6.8 (5–8)
	8	265	12	12	7.3 (3–14)	7.6 (4–15)
	9	270	10	12	7.8 (4–11)	12 (6–8)
	10	305	10	13	8.7 (4–13)	7.8 (2–12)
	11	310	8	8	8.8 (6–12)	8.1 (6–10)
	12	320	8	9	10.6 (7–19)	9.5 (5–19)
	13	335	12	9	10.7 (5–18)	12.4 (7–19)
	14	355	13	17	10.5 (7–16)	11.5 (5–24)
	15	385	12	10	12.6 (5–18)	12.1 (6–20)
Females:	1	175	1	1	5 (5)	3 (3)
	2	177	1	1	4 (4)	3 (3)
	3	190	2	1	5 (4–6)	7.5 (7.5)
	4	195	2	1	4.5 (3–6)	6 (6)
	5	198	1	1	5 (5)	6 (6)
	6	201	1	1	3 (3)	6 (6)
	7	205	1	3	3 (3)	6.3 (4–8)
	8	215	1	2	6 (6)	5 (5)
	9	225	2	3	3.5 (2–5)	4 (3–5)

considerable Jetting combined with Inking on the spawning grounds (especially among females) at the conclusion of mating, at the conclusion of laying an egg strand (Smale et al., in press), or when small fishes (*e.g.*, *Pagellus bellottii natalensis* and *Spondylisoma emarginatum*) nip at them in the water column (Sauer and Smale, 1993). Thus, it is used as a secondary defense in the form of Deimatic behavior; *i.e.*, behavior that threatens, startles, frightens, or bluffs a predator (McFarland, 1982; Hanlon and Messenger, in press).

Several components are used only by males during agonistic encounters. **Raised arm** is a unilateral raising of one of the first pair of arms, on the side towards the approaching squid; sometimes the tip is darkened. This component is seen during similar circumstances in *Loligo pealei* (Arnold, 1962), but not in other loliginids. **Downward V curl** is downward curling of the arms, which are parted equally and bilaterally into groups; it is common in most loliginids when they are alarmed (Moynihan, 1985). **Splayed arms** is a highly conspicuous posture in which all eight arms and the two tentacles are spread radially, with a bias laterally. It is common during agonistic

contests between males and may function in mate guarding. **Parallel positioning** is simply positioning parallel and laterally to another squid, with the arms in the same direction on each animal. **Fin beating** occurs during Parallel positioning and represents escalation of an agonistic encounter, because there is a transition from visual signaling to physical contact (DiMarco and Hanlon, unpub.; Hanlon and Messenger, in press); physical contact is mild and no obvious harm is done. **Jockeying** (from dictionary "to move by skillful maneuvering . . . to act trickily") is another component of agonistic encounters in which one male (the "intruder") attempts to maneuver over or under the "owner" male it is fighting and to get nearer the female. Conversely, **Parrying** (from dictionary "to ward off . . . to turn aside . . . by a defensive movement") refers to the swimming maneuvers used by the owner male to counter the approach efforts of the intruder male. Both maneuvers involve swimming finesse and influence the outcome of agonistic contests.

Several other components are associated with mating and egg laying. *Loligo vulgaris reynaudii* mates in three ways. **Head-to-head mating** is when the male and female face each other and entangle the arms; it is common in loliginids and is best illustrated by Drew (1911). This component is thought to be the only way in which males place spermatophores in a female's bursa copulatrix, which is a pouch for storing sperm. Head-to-head mating was not observed directly in our study, but most *Loligo vulgaris reynaudii* females already had spermatophores in the bursa. **Male parallel mating** occurs when the male swims beneath the female and grasps her with his arms and passes spermatophores to the mantle cavity near the oviduct; this is also common in loliginids and is illustrated in Drew (1911). **Male "sneak" mating**, newly discovered in this study, occurs when small "sneaker" or "satellite" males jet in very quickly and grasp females near the base of the first or second arms (*i.e.*, always from above), presumably to place spermatophores amidst the arms, where single egg strands are held and fertilized regardless of the mating method. The posture **Egg holding** is seen after the female has drawn the single egg strand out of the mantle. The first two pairs of arms are compressed dorsally, holding the eggs in some distinctive way, perhaps to fertilize them with sperm drawn from the bursa copulatrix. Alternatively, the eggs could already be fertilized from spermatophores placed near the oviduct during male-parallel mating, or sperm from sneaker males could fertilize some ova; none of this is yet understood. **Mate guarding** occurs when the male of a temporary mating pair accompanies the female to the egg mop (a collection of egg strands on the substrate) and remains a few centimeters above her until she deposits an egg strand into the mop. This is also common among loliginids (*e.g.*, Hurley, 1977; Griswold and Prezioso, 1981; Hanlon and Messenger, in press).

### Body patterns

**Chromic patterns** last for minutes or hours. When squids are calm they are usually in the **Clear** body pattern or Clear with **Dorsal stripe**. These are cases in which a single chromatic component acts as a body pattern.

**Acute patterns** last seconds or, rarely, a minute or two. **White Flashing** is a male-only pattern that is used during agonistic contests between males. It can be differentiated from Clear by three factors: (1) it is shown only for a few seconds; (2) the whiteness appears brighter than Clear, probably due to reflective iridophores also being expressed, in addition to chromatophores being retracted (*n.b.*, iridophores are cells that produce structural or reflected color as opposed to pigmentary color; they have recently been shown to be controlled actively by the animal, Hanlon *et al.*, 1990); and (3) it is intermittent and can even appear somewhat pulsating. **Dark Flashing** is the brief appearance of the dark chromatic component All dark, usually 2-3 times in succession over a few seconds. It is shown by both sexes: during agonistic contests between males, by females when fighting males approach too closely, and by females when they jet away from the eggs after depositing an egg strand. **Bands** have rarely been seen (see comments above). **Accentuated Oviducal Gland** and **Accentuated Testis** are shown briefly by females and males, respectively, during courtship or during agonistic contests in males. There are other occasions in which single dark components are shown alone, but these were rare in our observations and cannot be described in any detail.

The **Blanch-Ink-Jet Maneuver** may be universal in squids inhabiting the photic zone: the animal blanches Clear and jets away quickly in the backwards direction while ejecting ink in a pseudomorph that remains in the same approximate position from which the squid started the maneuver. The pseudomorph resembles the size and shape of the dark squid that was just there. This is a secondary defense against predation (when, for instance, crypsis fails) and represents a typical escape response to attacking predators (Hanlon and Messenger, in press). Such behavior is called protean behavior because the variable and erratic escape response upsets target prediction by the attacking predator (Driver and Humphries, 1988).

**Lateral Display** is a complex behavior performed only by males in agonistic contests. It is somewhat stereotyped, but there is variability in the details and in the order in which components are shown. It begins with Parallel positioning by two males and then includes various visual signals of Arm spots, Fin spots, Infraocular spot, and Mantle margin stripe, accompanied by the postural components Raised arm or Splayed arms. There are then dy-

dynamic interactions that include White Flashing and Dark Flashing, and the contest can escalate to Fin beating followed by Jockeying by the intruder to get near the female, while the "owner" male Parries to keep the intruder away from her.

#### *Can body patterning ethograms help distinguish subspecies?*

The subspecies *Loligo vulgaris reynaudii* and *Loligo vulgaris vulgaris* are separated mainly by club sucker dentition and protein electrophoresis (Augustyn and Grant, 1988), and the subspecies seem to overlap in the region of West-Central Africa. We do not know whether their body patterns (and thus their behaviors) are distinct. Unfortunately, *Loligo vulgaris vulgaris* has only been studied briefly in the laboratory (Hanlon, 1988) so no comparison is possible. Therefore, we would appreciate information from biologists working with *L. v. vulgaris* off the Mediterranean or the Atlantic coasts from Europe to northwestern Africa (see distribution in Worms, 1983) about spawning locations that are comparable to that of *Loligo vulgaris reynaudii* in South Africa.

The data available for these two subspecies suggest that the chromatic component Mantle spots, seen in *Loligo vulgaris vulgaris* by Hanlon (1988), is unique to that subspecies. We would almost certainly have seen Mantle spots in our observations of *L. v. reynaudii*, since we commonly saw Fin spots, which are common in both subspecies. Conversely, the chromatic components Arm spots, Dark fins, Bands, Dark head and arms, Dark tentacle or arm tips, Accentuated testis, Accentuated oviducal gland, and Shaded oviducal gland of *Loligo vulgaris reynaudii* have not been reported in *Loligo vulgaris vulgaris* and should be searched for specifically in future work. Furthermore, the specific arrangement and length of the Lateral mantle streaks (see *Dark chromatic components* above and Table 1) should be compared carefully, because this component appears to be important in reproductive behavior, which is likely to be different in the two subspecies.

*Loligo vulgaris vulgaris* overlaps extensively with *Loligo forbesi* around European coastlines; thus a comparison of the chromatic components listed here with those listed by Porteiro *et al.* (1990) for *Loligo forbesi* might help to distinguish *Loligo vulgaris vulgaris* from *Loligo forbesi*. This is of major importance to fisheries biologists, who currently have no way to distinguish the two species with confidence either in the laboratory (with preserved specimens) or on board ship (with freshly caught animals). Making decisions for catch quotas and recruitment processes is impossible without certain identification of the species involved.

A similar study on *Loligo pealei* on its spawning grounds near Cape Cod in the Northeastern USA would

provide additional information on the visual signaling capability of that species, which, in addition to being commercially important (Summers, 1983), is used in biomedical and neuroscience research (Gilbert *et al.*, 1990).

#### *Behavioral diversity among loliginid squids*

The chromatic components of body patterns are particularly important because (1) they are discrete physiological entities under direct control by the CNS; (2) they are the primary components of the visual signal (*cf.*, Packard and Hochberg, 1977; Hanlon, 1982); and (3) they are specific to the organism, *i.e.*, they are genetically determined. As a general index of behavioral diversity, the number of chromatic components can be compared among various *Loligo* spp. (Hanlon and Messenger, in press): *Loligo vulgaris reynaudii* 23 (S. Africa), *Loligo plei* 20 (Caribbean), *Loligo forbesi* 17 (Europe), *Loligo vulgaris vulgaris* 16 (Europe), *Loligo pealei* 14 (northeastern USA), *Loligo opalescens* 13 (western USA). Not all species have been studied in comparable detail, but from familiarity with each species (RTH) this listing is basically correct insofar as the first two species show slightly richer repertoires of chromatic expression. Other genera in the Family Loliginidae such as *Lolliguncula* and *Alloteuthis* are substantially less rich, having only 12–13 chromatic components; furthermore, they have only two color classes of chromatophores (yellow and brown), compared to three (yellow, red, and brown) for *Loligo* and *Sepioteuthis* (Lipinski, 1985; Dubas *et al.*, 1986; Hanlon and Messenger, in press). In contrast, the loliginid *Sepioteuthis sepioidea* has 23 chromatic components and can project many rich combinations of these into numerous body patterns, producing far more diverse body patterning behaviors than any squid known (Moynihan and Rodaniche, 1982).

#### Conclusions

Nearly all of the components described in this study—29 of 36 (Table 1)—were involved in intraspecific behavior. It is predictable that many ritualized intraspecific visual signals will be found in squids because they are social animals with a complex mating system in which males compete for females, and both sexes are polygamous. Agonistic contests in male squids seem always to involve some variations of a Lateral Display, which is a form of "visual battle" used to establish or maintain dominance; this dominance presumably confers an advantage to males for temporary pairing and "preferred mating access" to females (DiMarco and Hanlon, unpub.; Hanlon and Messenger, in press).

None of the 36 components of patterning were completely unique to *Loligo vulgaris reynaudii* compared to other loliginid squids. We know of an analog for every



component (*cf.*, Hanlon, 1982, 1988; Moynihan, 1985; Porteiro *et al.*, 1990; Hanlon and Messenger, in press), although of course there will be detailed variations of each component that are species-specific. The more important differences between species are in the ways the components are combined into body patterns and used in different behaviors. The durations, frequencies, and sequences of components shown during different displays (*e.g.*, the Lateral Display during agonistic contests) will certainly be different in *Loligo vulgaris reynaudii* and in any other loliginid (*e.g.*, *Loligo plei*; DiMarco and Hanlon, unpub.). White Flashing has not been seen in other squids, although a similar behavior—called Lateral Silver—has been described in the loliginid *Sepioteuthis sepioidea*: it is a unilateral signal to repel rival males only in the latest stages of courtship (Moynihan and Rodaniche, 1982).

Our ethogram of body patterning behavior is reasonably complete for intraspecific components of body patterning. The direct observations amidst hundreds (sometimes thousands) of highly active squids on their spawning grounds provided more variety and the opportunity to see a wider range of behaviors than is possible in the laboratory. Furthermore, many of the intraspecific behaviors are highly stereotyped and were seen repeatedly. A greater amount of focal or behavioral sampling would certainly have yielded some new behaviors and should be attempted in the future. In addition, the behavior of *Loligo vulgaris reynaudii* should be recorded (1) during other stages of the life cycle, and (2) during dusk and dawn, as well as at night (using light intensifiers) so that other components and body patterns used for crypsis or predator evasion can be observed. Only 7 of 36 components were noted during behaviors other than intraspecific: Clear, Dorsal mantle collar iridophores, Dorsal mantle splotches, Bands, Shaded eye, Inking, and Jetting. Younger squids are generally found farther offshore, and the probability of observing them is lower (Augustyn, 1991). The hand-held video technique is preferable to using ROVs at night because the bright lights on the vehicle are unnatural and the ROVs are not nearly as maneuverable as a diver-held camera.

We cannot overemphasize the importance of studying behavior in the natural environment despite its difficulties. In the marine environment around southernmost South Africa, the cold rough waters and the relatively deep diving (usually about 25 m) resulted in short dives (about 30–40 min) that limited observations even when the water was somewhat clear and the squids were most active; on many dives subsequent to these, no squids were found or visibility was close to zero. Nevertheless, this is a good location for behavioral studies when conditions permit because squids are rather concentrated along the coast. Video was absolutely imperative because it maximized data acquisition and proved far superior to underwater

note taking and still photography as a means of recording and analyzing the body patterns accurately. The zoom capability of the video allowed a variety of sampling techniques: scan, focal, behavior, or *ad libitum*. Many details and pleasant surprises emerged from the tapes during analysis. For example, previous studies with the stationary ROV (Sauer *et al.*, 1992) revealed only seven chromatic components of patterning, whereas the present study, with diver-controlled video, revealed 23 chromatic components. This is because divers could scan the scene, anticipate behavioral sequences, and use focal or behavior sampling to follow either (a) mating pairs, (b) large lone males, or (c) small lone “sneaker” males, all of which were engaging in different types of behavior.

The chromatic components are taxonomic characters useful for distinguishing at the species (*e.g.*, Hanlon, 1988; Roper and Hochberg, 1988) and possibly the subspecies level (this paper). Because the chromatic components are genetically coded physiological entities, they are as appropriate as any morphological character. In particular, the taxonomy of the Family Loliginidae is confused, especially at the generic level. *Loligo* spp. are so similar in general appearance—especially after preservation—that these physiological chromatic components in the living animals may be better diagnostic characters than the traditional morphological ones. For the future, combining traditional morphological data with body patterning and behavioral data and eventually with molecular data (Kuncio and Hanlon, 1991; Brierley *et al.*, 1993) will certainly be required to resolve these taxonomic questions.

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